FEEDING ECOLOGY OF BLACK OYSTERCATCHER

(*HAEMATOPUS BACHMANI*) CHICKS

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A

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Abstract

The Black Oystercatcher is an internationally recognized bird species of conservation concern and the focus of multiple monitoring programs due its small global population size, restricted range, vulnerability to human and natural threats in nearshore marine ecosystems, and the important role it plays as a top-level consumer in the intertidal food web. I studied a population of Black Oystercatchers in Kenai Fjords National Park, Alaska in 2013 and 2014, examining variation in chick diet, assessing methods used to monitor diet, and investigating the influence of provisioning on brood survival. To better understand the biases and limitations associated with the quantification of prey remains, I compared diet estimates from prey remains with two other methods: direct observation of adults feeding young, and diet reconstruction by stable isotope analysis. Estimates from collected prey remains over-represented the proportion of limpets in the diet, under-represented the proportion of mussels and barnacles, and failed to detect soft-bodied prey such as worms. I examined age- and habitat-specific variation in chick diet and found no relationship between diet and age of chicks; however, diet differed between gravel beach and rocky island nesting habitats. To determine the importance of diet on brood survival, I modeled daily survival rates of broods as a function of energy intake rate and other ecological factors and found that broods with higher intake rates had higher growth rates and daily survival rates. Given the consequences of reduced energy intake on survival, changes in the abundance and composition of intertidal macroinvertebrates as a result of climate change may have significant impacts on Black Oystercatcher populations. These findings highlight the importance of diet and provisioning to chicks and identify limitations of using prey remains to characterize Black Oystercatcher diet.

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General Introduction

The Black Oystercatcher (*Haematopus bachmani*) is a large shorebird (Order: Charadriiformes, Family: Haematopodidae) distributed along the Pacific coastline from Baja California to the Alaska Peninsula and the Aleutian Islands. In late spring, individuals form pair bonds and defend composite feeding and nesting territories. Females lay one to three eggs in a shallow depression on the ground in a variety of habitats including gravel and sandy beaches, rocky islands and islets, exposed rocky headlands and sheltered tidal flats (Andres and Falxa 1995). Black Oystercatchers are monogamous and exhibit bi-parental care in which parents share incubation duties throughout the 27-day incubation period and raise their semiprecocial chicks together (Webster 1941; Hartwick 1976; Groves 1984). Parental feeding of offspring occurs shortly after hatch until well after time of first independent flight, which occurs when the chicks are approximately 40 days old (Andres and Falxa 1995). The species has a long life span with records of banded individuals living up to 15 years (Andres and Falxa 1995). Although longevity is high, annual reproductive success is generally low; in Alaska, the number of chicks produced annually per breeding pair ranges from 0.29 – 0.68 (Andres and Falxa 1995).

Ecologically, the Black Oystercatcher plays an important role in intertidal communities throughout the eastern Pacific shorelines of North America. The species feeds heavily on marine intertidal macroinvertebrates including mussels (genera: *Mytilus, Modiolus),* limpets (*Acmaea, Lottia, Tectura*), and chitons (*Katharina, Tonicella,* etc.). As a top-level consumer in the intertidal food web, the Black Oystercatcher can produce effects that cascade down trophic levels, influencing the structure of nearshore marine systems (Vermeer et al. 1992; Tessler and Garding 2006; Bodkin 2011). Oystercatcher foraging in winter, when individuals form large flocks, decreases limpet population density and the intensity by which limpets graze on algae,

resulting in increased algal abundance (Frank 1982; Hockey and Branch 1984; Lindberg et al. 1987). This effect has also been observed with breeding pairs of African Black Oystercatchers (*H. moquini;* Hockey and Branch 1984)). Thus, the cascading effects of oystercatchers on algae, mediated by reductions in limpets, can promote the abundance of an important primary producer that forms the base of many nearshore marine food webs.

While intertidal communities are shaped by oystercatchers, oystercatchers are conversely reliant on intertidal and shoreline habitats for all critical life history components, including breeding, nesting, foraging and raising young (Webster 1941; Andres 1998; Tessler and Garding 2006). Because of their reliance on these habitats, oystercatchers are vulnerable to natural and human-induced disturbances that occur within nearshore systems (Andres and Falxa 1995; Morse et al. 2006). Shoreline contamination can dramatically decrease nest occupancy, productivity, and feeding rates of Black Oystercatchers (Andres 1997). Additionally, global climate change can have profound effects on both oystercatchers and their prey. Sea level rise may decrease the availability of suitable nesting habitat. Furthermore, the effects of climate warming in the marine environment may lead to cascading effects up nearshore marine trophic webs ultimately impacting Black Oystercatcher populations (Tessler et al. 2014).

In addition to being reliant on nearshore marine habitats and vulnerable to changes within nearshore systems, Black Oystercatchers also have a small estimated global population size of ~ 10,000 (Andres et al. 2012). Because of these reasons, in addition to uncertainty in population trends, Black Oystercatchers are recognized as a species of conservation and management concern by numerous groups and agencies. They are listed as a bird of conservation concern by the U.S Fish and Wildlife Service, a species of high concern by the Canadian Wildlife Service, and are included in the Audubon Alaska WatchList (Donaldson et al. 2000; U.S. Fish and

Wildlife Service 2008; Kirchhoff and Padula 2010). Furthermore, they been included in monitoring programs and research efforts by the U. S. Forest Service and the National Park Service (U.S. Forest Service 2002; Bodkin 2011).

The Nearshore Vital Signs program, developed by the National Park Service's Southwest Alaska Network parks, is an important regional monitoring plan that includes Black Oystercatchers (Bodkin 2011; Coletti et al. 2011). The program monitors 'vital elements' in the nearshore trophic web, from primary producers to apex predators. Black Oystercatchers are included as a vital element due to their role as a top-level consumer in the intertidal, their sensitivity to disturbance, and their reliance on nearshore habitats for all critical components of their life history. Estimates of Black Oystercatcher population density, nest density, productivity, and prey species and sizes provided to chicks are obtained annually from a single visit during the summer to Kenai Fjords and Katmai National Parks. However, estimates obtained in this manner may be subject to potential biases such as collection date, prey body type, nesting habitat and chick age. These issues need to be accounted for in order to ensure accurate and robust interpretation of observed trends in monitoring data of Black Oystercatchers.

I conducted a two-year study of a population of Black Oystercatchers in Kenai Fjords National Park to fill knowledge gaps in the feeding ecology of Black Oystercatcher chicks and provide the Park Service with information to make better decisions with respect to oystercatcher management. In the first chapter of my thesis, I characterized diet of Black Oystercatcher chicks using three methods: quantification of prey remains at nest sites (the method used by the Park Service's monitoring program), direct observation of adults feeding young, and diet reconstruction by stable isotope analysis. I compared diet estimates from the quantification of prey remains with the two other methods to better understand the biases and limitations

associated with the quantification of prey remains. Additionally, I examined age- and habitat-specific variation in chick diet. For my second chapter, I calculated the energy content of oystercatcher prey and examined how energy intake rate influences the growth and survival of chicks. To provide insight into how parents meet the increasing nutritional needs of chicks, I examined how delivery rates, prey type and size vary with chick age.

Results of this research will ensure more accurate and robust interpretation of observed trends in monitoring data of Black Oystercatchers and refine our understanding of factors that limit breeding productivity of Black Oystercatchers in south-central Alaska. Additionally, this study will fill information gaps in the feeding ecology and energetics of Black Oystercatchers, particularly those relating to chick diet. Understanding the relationship between Black Oystercatchers and the macroinvertebrates on which they feed is essential in determining the energetic flow of trophic levels in the intertidal food web and will allow us to better interpret and predict the dynamics of intertidal communities.

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Chapter 1. Are prey remains accurate indicators of chick diet? Implications for long-term monitoring of Black Oystercatchers[1]

1.1 Abstract

The quantification of prey remains at a nest is a common method for estimating the diet of a variety of birds, including Black Oystercatcher chicks. However, these estimates may be subject to biases based on prey body type, nesting habitat, and collection date. To better understand biases and limitations associated with this method, we compared it with two other methods commonly used to characterize diet: direct observation of parents feeding young and diet reconstruction by stable isotope analysis. In 2013-14, we monitored 20 broods in Kenai Fjords National Park and adjacent islands using all three methods. Estimates from collected prey remains over-represented the proportion of limpets in the diet (63% for prey remains vs. 38% and 43% for observations and stable isotopes, respectively), under-represented the proportion of mussels (34% vs. 37%, 43%, respectively) and barnacles (1% vs. 6%, 8%, respectively), and failed to detect soft-bodied prey such as worms. On rocky islands, where chicks are confined to a small area around the nest, there were significantly greater numbers of prey remains than on gravel beaches, where chicks leave the nest site within days of hatching. For researchers using prey remains to monitor long-term trends in diet, we suggest that they focus efforts on areas, such as rocky islands, where chicks are confined to the nest site for a long proportion of the brood-rearing period. Although not true reflectors of diet, prey remains can function as rough indicators of diet and can serve as useful tools in several applications of diet studies, provided that biases are accounted for.

[1]Robinson, B. H., L. M. Phillips, H. A. Coletti, A. N. Powell. Are prey remains reliable indicators of chick diet? Implications for long-term monitoring of Black Oystercatchers. Submitted to the Journal of Field Ornithology.

1.2 Introduction

The quantification of prey remains at a nest is a common method for estimating the diet of predatory birds that discard uneaten prey or regurgitate pellets, including raptors, wading birds, shorebirds, gulls and corvids (Stiehl and Trautwein 1991; Schmutz and Hobson 1998; Redpath et al. 2001; Boyle et al. 2012). Prey remains can contain a wealth of ecological information, shedding light on trophic interactions, feeding energetics, niche relationships, and shifts in both prey and predator populations (Furness and Camphuysen 1997; Kohler et al. 2011; Boyle et al. 2012). However, prey remains often lead to estimates of diet composition that are biased according to prey type. For example, estimates of prey remains of raptors typically over-represent birds and under-represent small mammals and reptiles with inconspicuous bones (Simmons et al. 1991; Redpath et al. 2001; Bakaloudis et al. 2012). For gulls, estimates are often biased towards hard-bodied prey while soft-bodied prey such as fish and zooplankton are under-represented (Lindsay and Meathrel 2008; Weiser and Powell 2011). Similar bias towards hard-bodied prey may exist when applying this method to the invertebrate-based diets of shorebirds, including Black Oystercatchers (*Haematopus bachmani*).

The Black Oystercatcher is a common member of intertidal communities along the Pacific coast of North America. They feed exclusively on marine macroinvertebrates and are dependent on intertidal and shoreline habitats for all critical life history components, including breeding, nesting, foraging, and raising young (Webster 1941; Andres 1998). Because of their reliance on these habitats, Black Oystercatchers are vulnerable to natural and human-induced disturbances that occur within nearshore systems (Andres and Falxa 1995; Morse et al. 2006). Shoreline contamination can dramatically decrease feeding rates and productivity of Black Oystercatchers (Andres 1997). Additionally, global climate change may have profound effects

on both oystercatchers and their prey. Changes in the ocean chemistry, circulation, and temperature can have direct effects on performance and survival, potentially leading to shifts in species distributions, population dynamics, and trophic interactions. These shifts can result in large-scale community-level changes (Harley et al. 2006). Due to natural and human threats to coastal habitats, a restricted range, and a small global population size, Black Oystercatchers are recognized as a species of conservation and management concern by federal and state agencies and have been the focus of various monitoring programs and research efforts (U.S. Fish and Wildlife Service 2008; Tessler et al. 2010, 2014; Bodkin 2011).

In Alaska, prey remains have been used by the National Park Service to monitor Black Oystercatcher chick diet in order to identify factors limiting survival and productivity. While the diet of adult Black Oystercatchers in Alaska has been well studied, there is little known with respect to diets of chicks (but see Webster 1941; Andres 1998). The Nearshore Vital Signs program, developed by the National Park Service's Southwest Alaska Network (SWAN), is a regional long-term monitoring plan that includes estimates of intertidal invertebrate abundances and densities, as well as estimates of diet of Black Oystercatcher chicks. Diets are estimated from the quantification of prey remains obtained from a single visit to Kenai Fjords and Katmai National Parks during each breeding season (Bodkin 2011; Coletti et al. 2011). These estimates are used to detect spatial and temporal trends in chick diet and understand how changes in prey composition and abundance influence oystercatcher survival and productivity.

The quantification of prey remains near Black Oystercatcher nests is a simple and efficient method that has been used to estimate chick diet for decades (Webster 1941). This method works well with Black Oystercatcher chicks due to their semi-precocial nature; chicks are born fully feathered but rely on prey brought to them by their parents throughout the 40-day

brood-rearing period (Andres and Falxa 1995). Following the SWAN Black Oystercatcher monitoring protocol, researchers typically visit nests once per breeding season and collect all the prey remains within 10 m (Bodkin 2011). Although the quantification of prey remains is a widely-used method for estimating diet composition of Black Oystercatcher chicks, these estimates may be subject to biases based on prey body type, nesting habitat, and collection date. For example, soft-bodied prey lacking shells, such as marine worms, may go undetected (Lindsay and Meathrel 2008). Further, Black Oystercatcher chicks are highly mobile and do not remain at the nest throughout the entire brood-rearing period unless constrained by their nesting habitat. For example, at nests on rocky cliffs or islets, chicks may be confined to the area immediately around the nest throughout the breeding season. However, in open habitats such as gravel beaches, chicks can leave the nest a few days after hatch and follow their parents to intertidal feeding areas; thus, prey collected around the nest would only represent diet during a brief time window. Additionally, prey brought to chicks reflects diet only prior to the collection date. Peak hatch occurs around 10 June and for the SWAN monitoring program a single visit to each nest occurs after 15 June of each year, as near as possible in time to visits in previous years (Bodkin 2011). However, because monitoring protocols only collect prey remains once per season, any changes in diet after collections are made will be missed. These biases (prey body type, nesting habitat, and collection date) may lead to inaccurate conclusions of dietary trends, yet no studies have investigated how prey remains compare to the true diet of Black Oystercatcher chicks.

Another commonly used method of characterizing the diet of birds is through direct observation of feeding (Hutt and Hutt 1970). Observer bias, including inability to correctly identify prey, may lead to errors resulting in imprecise estimates if this method is employed.

Further, direct observations reflect point-in-time dietary information and therefore require substantial observations to determine temporal changes in diet. Despite these issues, direct observation is considered to be the most accurate method of estimating diet (Marti et al. 2007; Bakaloudis et al. 2012).

Stable isotope analysis is a powerful tool that indirectly estimates diet composition (Parnell et al. 2013; Phillips et al. 2014). This method exploits the fact that stable isotopes in prey sources are transferred in a predictable manner to a consumer when eaten and ratios of stable isotopes vary among prey items. Carbon isotopes provide information on the source of primary production and nitrogen isotopes reflect the trophic level of consumed prey (DeNiro and Epstein 1978; Minagawa and Wada 1984; Bearhop et al. 2002). Isotopic mixing models estimate the proportional contribution of prey items within a consumer's tissues (Parnell et al. 2010). An advantage of this method is that researchers can obtain short- or long-term dietary information depending on the consumer tissue they choose to sample because dietary estimates are based on assimilated prey, and different consumer tissues have different rates of assimilation (Hobson and Clark 1992). This analysis is invasive, requiring tissue samples to be collected, which involves capture and handling of birds. Additionally, preservation of tissue samples and additional procedures, such as centrifuging blood, can be logistically complicated, particularly in remote areas. Further, isotopic mixing models do not perform well if prey items are not isotopically distinct. Despite these factors, stable isotope analysis has been used to characterize diet in numerous bird studies and successfully used to estimate the diet composition of adult Black Oystercatchers in the northern Gulf of Alaska (Inger and Bearhop 2008; Carney 2013).

The objectives of this study were to 1) characterize the diet of Black Oystercatcher chicks in south-central Alaska utilizing three methods: quantification of prey remains, direct

observation, and stable isotope analysis, 2) compare diet estimates from prey remains with estimates from direct observation and stable isotope analysis, and 3) examine age- and habitat-specific differences in diet using the three methods. We predicted that estimates of diet from the quantification of prey remains would be biased based on prey body type when compared with the other two methods, given the potential biases associated with prey remains and previous studies showing that direct observation and diet reconstruction by stable isotope analysis can provide accurate estimates of diet. Specifically, we predicted estimates based on prey remains would under-represent the proportion of soft-bodied prey, such as marine worms, when compared to estimates obtained from direct observation and stable isotope analysis. Furthermore, we predicted that if the diet of chicks changed with age, then estimates based on prey remains would only represent the diet of chicks until the date of collection. However, we would only expect to see such bias for chicks that nest on open beaches, where they may leave the nest very early in the brood-rearing period.

1.3 Methods

We conducted field work in Aialik Bay within Kenai Fjords National Park in south-central Alaska, U.S.A., from May to August in 2013 and 2014 (59°51'18"N, 14°942'14"W; Fig. 1.1). Aialik Bay is a deep, glacially-forged inlet, 35 km in length, in-cut by smaller coves and bounded by steep mountains extending to 1478 m (Cook 1998; Spencer and Irvine 2004). Shoreline topography varies from gravel beaches of low-wave energy to rocky cliffs of high-wave energy with a mean tide range of 1.7 m (NOAA 2008). Nesting habitat in our study site can be classified into two general categories: gravel beaches, which consists of mixed sand and

gravel or mixed cobble and gravel beaches, and rocky islands, which include rocky islets or wave-cut platforms on islands.

In May of each year, we conducted systematic boat-based surveys of historically known nesting sites to locate breeding territories. Upon detecting a territorial pair of Black Oystercatchers, we searched the surrounding area on foot. If an active nest was found, we recorded clutch size and floated eggs to determine the stage of incubation (Mabee et al. 2006). Throughout the course of the breeding season we periodically revisited sites where nests had failed, sites where territorial pairs were observed but had yet to initiate a nest, and historical breeding sites to detect new nests. We monitored nests every three to five days throughout the nesting period. As nests approached the estimated day of hatch, we visited them daily to determine hatch date. After eggs hatched, we monitored broods to collect prey remains, conduct observations, and collect blood samples. We monitored six broods in 2013 and 14 broods in 2014 (Fig. 1.1). In 2014, we expanded our study area to include islands adjacent to Aialik Bay. Four of the broods from 2014 were from nests on rocky islands; all other broods, from 2014 and 2013, were from nests on gravel beaches.

1.3.1 Prey remains

We collected the remains of prey provisioned to chicks at nests, following a pre-established protocol designed for monitoring Black Oystercatcher chick diet in Katmai and Kenai Fjords National Parks (Bodkin 2011). To avoid attributing old prey remains to an active brood, we visited nests during the incubation period and removed and discarded all prey remains within ~ 10 m of the nest site. From the time of hatch until chicks fledged or failed, we visited nests every three to five days to search for prey remains. We collected all prey remains found within ~ 10 m of the nest site and later identified them to the genus or species level. We did not collect prey

remains >10 m from the nest. In most cases, after the chicks moved away from the nest, they followed their parents into the intertidal zone to be fed. Any prey remains discarded in the intertidal would get washed away with the incoming tide.

1.3.2 Direct observations

We conducted direct observations of each brood approximately every three to five days until they fledged or failed. We observed adults feeding chicks during low tide when intertidal feeding grounds became exposed. Observations were standardized to a two-hour duration, centered on the time of low tide. Upon arriving at a territory, we located the brood from our boat using binoculars. During the first few days after hatch, broods remained at the nest but later (with the exception of chicks on rocky islands) they moved with their parents to intertidal feeding areas and throughout their territory. After a brood was located, we set up a camouflaged blind ~ 50 m from the birds. We then waited for the birds to resume normal activity, which typically occurred within minutes of entering the blind. We watched the brood with a 20-60x spotting scope and recorded each prey item fed to a chick. Prey items, in general, were easily identifiable to the genus or species level based on shape, size and color of the prey, and handling behavior of the adults. If the observer was unsure of the prey or vision was obstructed during a feeding event, the prey item was listed as 'unknown'. Two observers worked together throughout the study to reduce observer bias.

1.3.3 Stable isotope analysis

We collected prey samples and blood plasma from chicks for diet reconstruction by stable isotope analysis. We used blood plasma for analysis because it yields relatively short-term dietary information of approximately one week (Hobson and Clark 1993). From late June to late July, we captured chicks by hand during high tide when intertidal feeding areas were submerged

to minimize disturbance to feeding. We marked chicks with colored tape or colored plastic bands until their tarsi were large enough to be fitted with a U.S. Geological Survey (USGS) metal band and two plastic alpha-numeric bands. We captured each chick twice, once during the early brood-rearing phase (~ 10-15 days after hatch) and again during the late brood-rearing phase (~ 20-30 days after hatch).

We collected ≤ 10 µl of blood from the brachial vein of chicks using sterile 27-gauge hypodermic needle bevels and heparinized microcapillary tubes. Within four hours of drawing blood, we separated plasma from red blood cells with a Fisher Scientific Mini-Centrifuge (Pittsburgh, PA) by centrifuging for 10 min at ~ 6,200 rpm. We transferred the separated plasma to cryogenic vials and stored them in a freezer for the duration of the field season.

We collected intertidal invertebrates to provide a reference of prey items for stable isotope analysis. We sampled from four intertidal feeding areas during low tide in July 2013 (Fig. 1.1). In July 2014, we sampled at the same four locations and included a fifth sampling location to reflect our expanded study area. We collected invertebrate samples that represented taxa and size classes of prey items observed during provisioning events. We gathered a minimum of five samples per prey item if they could be found at the sampling location. We limited the taxa that we collected to the six most common prey types (listed in Table 1.1). In a stable isotope mixing model, including too many prey sources will prevent finding a unique solution to source proportions (Phillips and Gregg 2003; Phillips et al. 2014). Although some taxa were excluded from the stable isotope analysis that were detected during prey collections or observations, they each represented less than one percent of the diet based on either prey remains or observations. Samples were stored for approximately one month in plastic bags in a freezer prior to being transported, in ice, to Fairbanks for laboratory analysis.

We determined the carbon and nitrogen stable isotope ratios of blood and prey samples at the Alaska Stable Isotope Facility. We analyzed five samples per prey item per location in 2013 and three samples per prey item per location in 2014. We freeze-dried blood and prey samples and removed shells from prey, and then homogenized prey samples using a mortar and pestle or an amalgamator. We collected 51 samples of blood plasma from 28 chicks, but only 39 samples were analyzed due to equipment malfunction. Stable isotope values were obtained using continuous-flow isotope ratio mass spectrometry with a Costech ESC 4010 elemental analyzer and Thermo Scientific Conflo IV interfaced with a Thermo Scientific DeltaV^{Plus} Mass Spectrometer. Stable isotope ratios are reported in δ notation as parts per thousand (‰) deviation from the international standards (Vienna-PeeDee Belemnite for carbon and atmospheric air for nitrogen) according to the following equation: δX (‰) = ([$R_{sample}/R_{standard}$]-1) x 1000, where X denotes either ^{13}C or ^{15}N and R represents the ratios of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ in relation to the respective standards. Analytical precision, measured as the standard deviation of known laboratory standards (peptone $\delta^{13}C$ = -15.8 and $\delta^{15}N$ = 7.0) run concurrently with samples, was 0.2 ‰ for carbon and nitrogen.

1.3.4 Statistical analysis

Each method we used to estimate diet provided information over a different time scale: two hours for observations, three to five days for prey remains, and approximately one week for stable isotope analysis. To allow for comparison among methods of different time scales, we integrated data over the entire season for each method. We also examined temporal trends by comparing diet between the early and late brood-rearing period.

We determined the composition of prey remains for each brood by expressing the number of prey remains for each prey type as a percentage of the total number of prey remains for all

prey types. We averaged across broods of both years to obtain a composition of prey remains for the overall population. We determined the composition of prey fed to chicks for each brood in the same manner. We examined habitat differences first by testing for differences in the number of prey items collected at nest sites on rocky islands versus gravel beaches using a Wilcoxon rank sum test. We used a Pearson's Chi-squared to test for differences in the composition of prey items between rocky island and gravel beach nest sites, for both prey remains and direct observations, However, due to our small sample size (with expected frequencies less than 5.0), we computed the sampling distribution of the test statistic by Monte Carlo simulations with 100,000 replicates. We also used a Pearson's Chi-squared with 100,000 replicates to test for differences in the composition of prey items fed to chicks during early and late-brood rearing periods.

To estimate the fractional contribution of prey items in the diet of chicks, we used the hierarchical Bayesian stable isotope mixing model MixSIAR, which incorporates standard deviations of mean prey sources and consumer signatures and allows for uncertainty regarding diet-consumer discrimination values (Semmens et al. 2009; Parnell et al. 2013; Stock and Semmens 2013). In our analysis, tissue samples of chicks were paired with tissue samples of invertebrates from the nearest sampling location to account for site-specific differences in the isotopic signatures of prey. If the number of prey sources included in a mixing model is high or the isotopic signatures of prey sources overlap, the discriminatory power of the model is reduced (Phillips et al. 2014). However, the incorporation of prior information to mixing models in a Bayesian framework can increase the power to discern source contributions (Moore and Semmens 2008). We used informative priors, based on the prey proportions from our direct observations, to guide model estimates of prey contributions to consumers. In addition to

estimating the composition of a population's diet, MixSIAR estimates the variation in diet within the population by calculating posterior distributions of estimated variability for given factors (Semmens et al. 2009). Because we reasoned that diet might vary according to habitat, age of chick (early vs. late brood-rearing period), and among individuals, we included these three factors in our model. We used a trophic enrichment factor (TEF) of ($\Delta \pm$ SD) 0.02 ± 0.40 ‰ for ^{13}C and 4.05 ± 0.60 ‰ for ^{15}N, based on a captive feeding trial of adult Black Oystercatchers in Seward, AK (Carney 2013). Because the TEF of the feeding trial was calculated for whole blood and not plasma, we corrected for plasma by subtracting the difference in the TEF between whole blood and plasma for Dunlin (*Calidris alpina*) from the TEF of Black Oystercatcher whole blood (Evans Ogden et al. 2004). Also, because growth induces a depletion in $\delta^{15}N$ value, we corrected for age using the slope of a regression of $\delta^{15}N$ and age up to 50 days, when chicks stop growing (Sears et al. 2009; values shown in Table 1.2).

We tested for differences in the composition of prey items between direct observation and prey remains using a Pearson's Chi-squared test with a Monte Carlo simulated test statistic based on 100,000 replicates. We could not include diet estimates from stable isotope analysis in the Chi-squared test because they are not frequency data; therefore we compared the composition of prey among all three methods. All statistical analyses were conducted in program R, version 3.1.1, using an α-level of 0.05 (R Development Core Team 2014).

1.4 Results

1.4.1 Prey remains

We collected 2126 prey remains from the 20 nests monitored. Prey remains consisted primarily of limpet (*Lottia* spp., *Acmaea mitra*) shells (63%), followed by mussel (*Mytilus trossulus*) shells

(34%), barnacle (*Semibalanus cariosus*) shell plates (1%), snail (*Nucella* spp.) shells (1%), chiton (*Katharina tunicata*, *Tonicella* spp.) girdles and plates (1%), and isopod (*Ligia pallasii*) exoskeletons (< 1%; Fig. 1.2). Prey remains differed by nesting habitat. There were greater numbers (mean ± SD) of prey remains at nests on rocky islands (417 ± 383) than gravel beaches (4 ± 3; Wilcoxon rank sum test: $W = 0$, $P = 0.002$). The composition of prey items also differed between rocky island and gravel beach nest sites ($\chi^2 = 25.83$, B = 100000, $P = 0.01$). Mussel remains were disproportionately more common on rocky islands (42% at islands vs. 30% at beaches) while limpet remains were disproportionately more common on gravel beaches (65% at beaches vs. 56% at islands). During the late-brood rearing period, we only found prey remains at two of the 20 broods because broods had either failed or moved away from the nest site by then.

1.4.2 Direct observations

We observed 1979 prey items fed to chicks in the 20 broods monitored. Adults primarily fed chicks limpets (*Lottia* spp., *Acmaea mitra*; 38%) and mussels (*Mytilus trossulus;* 37%) and, to a lesser degree, barnacles (*Semibalanus* cariosus; 6%), chitons (1%), worms (*Nereis vexillosa;* 1%), snails (*Nucella* spp., *Cryptonatica* sp. ;<1%), rock jingles (*Pododesmus macrochisma*; <1%), and isopods (*Ligia pallasii*; < 1 %; Fig. 1.2). We were unable to identify 17% of the prey provisioned to chicks, primarily due to obstructions in vision during provisioning events. The composition of prey items fed to chicks differed between rocky island and gravel beach nest sites ($\chi^2 = 20.85$, B = 100000, $P = 0.02$), but these differences were small: the differences in the proportion of the prey items fed to chicks between island and beach sites was < 5% for all prey items. The composition of prey items fed to chicks did not differ significantly between the early and late brood-rearing period ($\chi^2 = 2.43$, B = 100000, $P = 0.79$).

1.4.3 Stable isotopes

We analyzed carbon and nitrogen isotope values of blood plasma sampled from 28 chicks from 20 broods to determine the proportional contribution of prey in the diet. Limpets (0.43 ± 0.05) and mussels (0.43 ± 0.05), made up the largest proportions (mean ± SD) in diet of the population, followed by barnacles (0.08 ± 0.03), chitons (0.03 ± 0.02), worms (0.02 ± 0.02), and snails (0.01 ± 0.01; Fig. 1.2). The majority of the variation in chick diet was explained by habitat. The posterior median of estimated variability among habitat ($\hat{\sigma}_{habitat} = 5.80$) was larger than variability between brood-rearing periods ($\hat{\sigma}_{age} = 4.62$) or variability among individuals ($\hat{\sigma}_{individual} = 0.99$). Habitat-specific differences in prey for stable isotopes followed a similar trend to that of prey remains: mussels were more common in the diet of chicks on rocky islands than gravel beaches (45% at islands vs. 39% at beaches) while limpets were more common in the diet of birds on gravel beaches than rocky islands (40% at beaches vs. 30% at islands). Carbon and nitrogen isotope values of Black Oystercatcher chicks and marine invertebrates are listed in Tables 1.1 and 1.2.

1.4.4 Comparison among methods

Estimates of prey consumed by chicks differed by methodology. The composition of prey items differed between direct observation and prey remains ($\chi^2 = 241$, B = 100000, $P < 0.001$). Estimates of prey remains over-represented the proportion of limpets in diet (63% for prey remains vs. 38% and 43% for observations and stable isotopes, respectively), under-represented the proportion of mussels (34% vs. 37%, 43%, respectively) and barnacles (1% vs. 6%, 8%, respectively), and failed to detect worms (Fig. 1.2).

1.5 Discussion

Our work provides the first comparison of methods used to estimate the diet of Black Oystercatcher chicks. Prey composition was relatively consistent between direct observation and stable isotope analysis, however it differed significantly between direct observation and prey remains. Diet also differed for chicks reared on gravel beaches versus rocky islands, based on all three methods. However, there was little difference in chick diet during the early versus late brood-rearing period.

Chicks were fed predominantly limpets and mussels, supplemented by a variety of other intertidal macroinvertebrates. To our knowledge, we provide the first documentation of oystercatcher chicks feeding on rock jingles (*Pododesmus macrochisma*). Our estimates of prey composition were similar to observations of prey consumed by chicks in Prince William Sound, Alaska, which consisted primarily of limpets (48%) and mussels (42%), in addition to chitons (3%) and clams (6%; Andres 1998). Estimates of diet based on direct observation at Cleland Island, British Columbia, Canada also indicated that mussels (40%) and limpets (37%) were the dominant prey items, followed by *Nereis* worms (7%) and crabs (6%), with all other prey items (snails, isopods and other worms) each representing less than 5% of the diet (Hartwick 1976). However, on the Gulf Island Archipelago, British Columbia, limpets were the most frequently delivered prey item (70%), followed by barnacles (13%), chitons (12%), and other prey (5%; Hazlitt et al. 2002). Collectively, these results underscore the importance of limpets and mussels as a food resource to Black Oystercatcher chicks throughout much of their northern range.

Consistent with our prediction that estimates of chick diet would be biased according to prey body type, we found that prey remains failed to detect soft-bodied prey, such as marine worms. The composition among hard-bodied prey items also differed between methods. Specifically, limpets were over-represented and mussels and barnacles were under-represented

by estimates of prey remains. These discrepancies can be explained by differences in the handling behavior of prey by adults. Hartwick (1976) described the attack behavior of oystercatchers on mussels as a stabbing action in which the bird draws out the meat with rapid levering and biting, and only occasionally does the bird carry away the whole mussel, shell included. Likewise, we observed that adults often removed the soft-bodied parts of barnacles and mussels on the feeding grounds, leaving the shell or shell plates attached to the substrate before flying back to provision their chick(s). When this occurred, there were no prey remains left at the nest to detect. However, with limpets, adults typically removed the entire organism from the substrate and returned to the vicinity of the chick(s), where they removed the shell and provisioned the young.

Furthermore, we found a two-orders-of-magnitude difference in the number of prey remains collected between nests at rocky islands and nests at gravel beaches. This difference can be attributed to the duration of time chicks spent at their nests. Chicks on rocky islands were confined to a small area for 20-30 days after hatch and therefore had a larger accumulation of prey remains at their nests. In contrast, chicks on gravel beaches left the nest site within one to three days of hatch, and therefore had much smaller accumulation of prey remains at their nests. Thus, prey remains collected on gravel beaches only reflect diet for the first few days after hatch. This finding illustrates one of the limitations of prey remains as indicators of diet.

Our findings demonstrate that chick diet was consistent throughout the brood-rearing period. We found no differences in diet between the early and late brood-rearing periods based on direct observations and stable isotope analysis. However, we did not test for a difference in prey remains because we only found prey remains during the late period for two of twenty broods monitored. In contrast, diet did vary by nesting habitat; estimates of prey composition

from both prey remains and direct observation differed between nests located on gravel beaches versus rocky islands. Similarly, for the stable isotope analysis, the majority of variation in diet was explained by nesting habitat. We found that mussels were more common in the diet of chicks on rocky islands whereas limpets were more common in the diet of chicks on gravel beaches. These habitat-specific variations in diet are likely a result of differences of prey availability and profitability. Mussel densities have been positively correlated with increasing wave action which may explain why mussels were more common in the diet of individuals that nested on rocky islands (Westerbom and Jattu 2006). The intertidal feeding areas at all of our rocky island sites were exposed to the Gulf of Alaska and had high wave action. Whereas all the feeding areas near the gravel beaches were sheltered from the Gulf of Alaska by islands and subject to lower wave action. Limpets were more common in the diet of individuals that nested on gravel beaches and have been found to be significantly larger in size in sheltered areas compared to exposed areas (Hobday 1995). Limpets may be consumed at sheltered gravel beaches more frequently than at rocky island sites because they are energetically more profitable prey due to their larger size and because mussels occur there at lower densities compared to the wave-exposed rocky islands.

Like any technique used to study diet, the quantification of prey remains has its advantages and disadvantages. A major disadvantage is that this method is biased according to prey body type. Although prey remains do not detect soft-bodied prey such as worms, in our study site worms made up a very small part of chick diet (2% from stable isotope analysis, 1% from direct observation). However, in other regions or in other oystercatcher species, this bias may have bigger implications. For example, some populations of Magellanic (*H. lecopodus*) and Eurasian (*H. ostralegus*) Oystercatchers exhibit diet dimorphism, in which individuals specialize

in either hard-shelled prey or soft-bodied burrowing prey (Swennen et al. 1983; Safriel 1985). Estimating diet by prey remains would overlook a significant portion of prey in these populations. For those monitoring diet in populations that feed heavily on soft-bodied prey, we recommend conducting direct observations or stable isotope analysis rather than collecting prey remains.

The other disadvantage of using prey remains to characterize diet is the short time-window that they reflect at gravel beach sites. For prey remains to be representative of diet for more than the first few days of a chick's life, studies should focus on populations that nest primarily on rocky islands and islets, where chicks cannot stray far from their nest. In the northern portion of their range, Black Oystercatchers nest on sand and gravel beaches in addition to rocky islands. For example, in our study site, 80% of nests occurred on gravel beaches, while only 20% occurred on rocky islands. In Prince Williams Sound, Alaska, nests were more evenly distributed between rocky (45%) and gravelly (55%) sites (Andres and Falxa 1995). However, in the California, U.S.A. and northern Baja California, Mexico, Black Oystercatchers nest primarily on rocky islands, islets and headlands (Tessler et al. 2014). The quantification of prey remains at these southerly sites would be more informative of chick diet throughout the brood-rearing period.

Despite these disadvantages, there are numerous advantages of using prey remains to determine composition of chick diet. Unlike stable isotope analysis, this technique is non-invasive and requires minimal disturbance to the birds. Also, prey remains can be collected by anyone regardless of skill or experience as opposed to direct observations, which require individuals with knowledge of marine intertidal invertebrates and the ability to quickly identify prey by sight. Furthermore, the quantification of prey remains is relatively inexpensive and can

be done in a short amount of time. The costs of labor and equipment for prey remain studies are a fraction of the costs of using stable isotope analysis. The collection of prey remains for our study took < 5 hours, while our observations took 210 hours. These advantages, particularly the inexpensive cost and short time required, make this an attractive method for various long-term diet studies.

In addition, the use of prey remains can be particularly useful for documenting changes in hard-bodied prey consumption within sites over time. In South Africa, stable isotope analysis was used to show a geographic shift in African Black Oystercatcher (*H. moquini*) diet related to the spread of the invasive Mediterranean mussel (*Mytilus galloprovincialis*; Kohler et al. 2011). Long-term monitoring of prey remains could reveal additional diet shifts elsewhere in the range of African Black Oystercatchers if Mediterranean mussels continue to expand. In Alaska, there has been an apparent decrease in percent cover of mussels in Kenai Fjords and Katmai National Parks, and Prince Williams Sound (H. Coletti, unpublished data). Monitoring prey remains over time can inform managers how oystercatchers are responding to these shifts in invertebrate abundance. Furthermore, monitoring prey remains may provide insight into factors limiting oystercatcher survival. The critical life history stage in oystercatchers is survival from hatch to fledge (Groves 1984) and low food availability can lead to low chick survival (Heg and van der Velde 2001). By detecting low relative abundance of prey remains, long-term monitoring of prey remains can be useful in identifying when chick survival may be compromised. However, prey remains need to represent chick diet throughout a substantial portion of the brood-rearing period, which is not the case with prey remains at nests on gravel beaches.

These examples illustrate the utility and limitations of prey remains in diet studies. While not true reflectors of diet, prey remains can provide valuable data with little cost and effort. However, biases should be accounted for before making interpretation of trends in the diet data.

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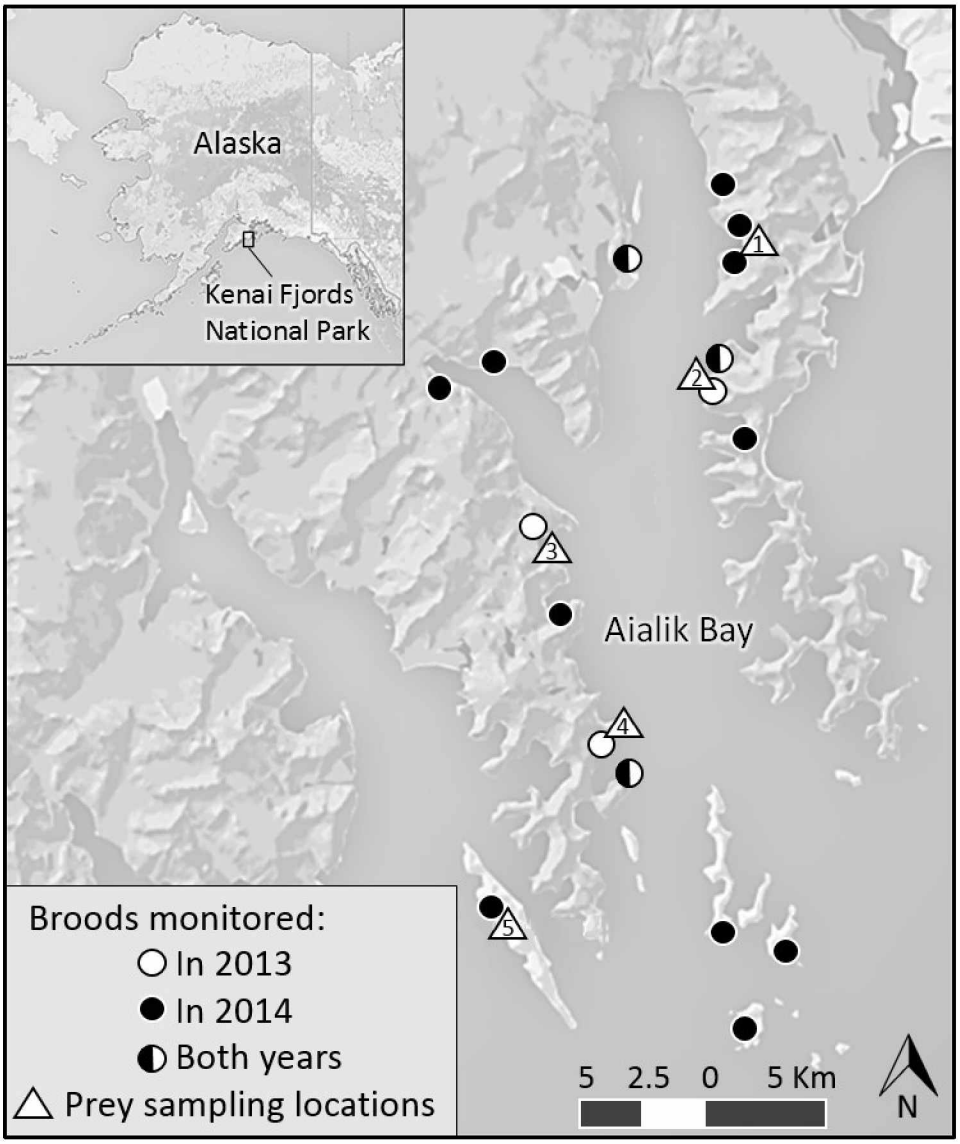

Figure 1.1. Locations of Black Oystercatcher broods monitored and sampling locations for invertebrate prey in Kenai Fjords National Park, Alaska, U.S.A., 2013-2014.

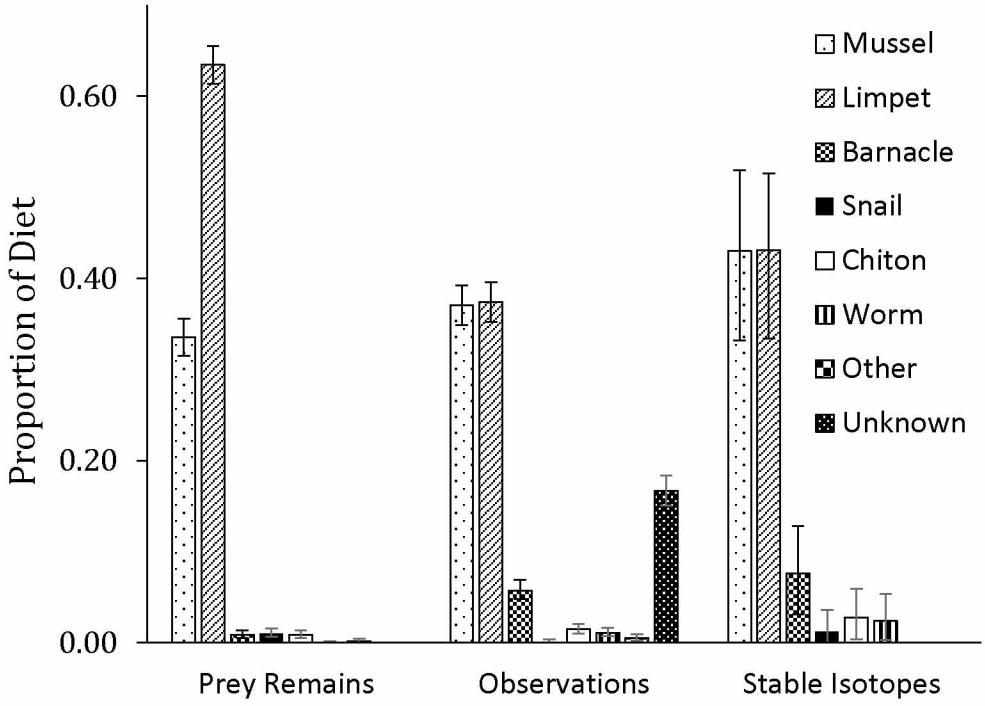

Figure 1.2. Proportion of prey items in the diet of Black Oystercatcher chicks based on method: diet reconstruction by stable isotope analysis of carbon and nitrogen, direct observation of adults feeding chicks, and quantification of prey remains at nest sites at Kenai Fjords National Park, Alaska, U.S.A., 2013-2014. "Other" category includes *Ligia pallasii*, *Cryptonatica aleutica*, and *Pododesmus macrochisma*. Error bars represent 95% confidence intervals for prey remains and observations and 95% credible intervals for stable isotopes.

Table 1.1. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values (mean ± SD) of marine invertebrates sampled in Kenai Fjords National Park, Alaska, U.S.A., 2013-2014.

	Location[a]	$\delta^{13}C$	$\delta^{15}N$	*n*
Katharina	1	-18.85 ± 1.27	8.16 ± 1.08	3
Katharina	2	-20.19 ± 1.15	8.22 ± 0.84	6
Katharina	3	-17.09 ± 0.71	8.20 ± 0.31	3
Katharina	4	-18.49 ± 0.50	7.43 ± 0.83	8
Katharina	5	-18.99 ± 0.40	9.90 ± 0.41	3
Lottia	1	-15.80 ± 0.70	7.92 ± 0.34	3
Lottia	2	-20.50 ± 0.64	6.60 ± 0.78	9
Lottia	3	-19.45 ± 1.07	7.10 ± 1.00	10
Lottia	4	-16.93 ± 1.83	7.89 ± 1.05	7
Lottia	5	-15.73 ± 0.36	7.15 ± 0.74	2
Mytilus	1	-19.55 ± 0.77	6.90 ± 0.76	3
Mytilus	2	-20.99 ± 0.37	7.15 ± 0.40	8
Mytilus	3	-20.95 ± 0.63	6.97 ± 0.36	10
Mytilus	4	-20.00 ± 0.41	7.63 ± 0.73	8
Mytilus	5	-19.73 ± 0.03	7.53 ± 0.53	3
Nereis	1	-18.85 ± 0.34	9.24 ± 0.37	4
Nereis	5	-19.46 ± 0.90	9.48 ± 0.55	3
Nucella	1	-17.91 ± 0.16	9.00 ± 0.33	7
Nucella	2	-18.71 ± 0.68	9.32 ± 1.01	10
Nucella	3	-19.08 ± 0.31	8.91 ± 0.44	14

Nucella	4	-18.64 ± 0.20	9.00 ± 0.19	3
Nucella	5	-18.02 ± 0.26	9.48 ± 0.45	3
Semibalanus	1	-18.47 ± 0.95	7.78 ± 0.03	3
Semibalanus	2	-18.51 ± 0.38	8.87 ± 0.66	8
Semibalanus	3	-19.39 ± 0.91	8.80 ± 0.45	8
Semibalanus	4	-18.69 ± 0.47	9.27 ± 0.31	7
Semibalanus	5	-16.65 ± 1.57	9.19 ± 0.53	3

[a]Prey sampling locations are shown in Fig. 1.1.

Table 1.2. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values of Black Oystercatcher chick blood plasma sampled in Kenai Fjords National Park, Alaska, U.S.A., 2013-2014.

Nest ID	Brood-rearing Period	$\delta^{13}C$	$\delta^{15}N$	Corrected $\delta^{15}N$[a]
01AB14	early	-20.61	9.01	10.67
01AB14	early	-20.14	10.44	12.10
02AB13	early	-20.08	11.21	12.83
02AB13	late	-20.45	9.56	10.95
02AB14	late	-20.32	9.30	10.87
02AB14	late	-20.34	9.82	11.39
02AB14	late	-19.28	11.18	11.94
03AB14	early	-19.62	9.71	11.51
03AB14	late	-19.67	9.91	10.49
03AB14	late	-19.50	10.75	11.33
04AB14	late	-20.69	10.13	10.80
04AB14	late	-20.21	10.13	11.30
06AB13	early	-19.39	11.07	12.87
06AB13	early	-19.37	11.14	12.94
06AB13	early	-19.21	11.32	13.12
08AB13	late	-19.09	11.98	12.61
08AB13	late	-18.85	12.39	13.56
08AB14	late	-19.37	9.92	10.77

08AB14	late	-19.10	9.91	11.44
08AB14	late	-19.01	10.21	11.74
09AB14	early	-19.12	8.61	10.36
09AB14	early	-19.09	9.63	11.38
10AB13	late	-20.33	10.25	11.78
10AB13	late	-19.73	11.04	11.89
10AB13	late	-19.92	10.52	12.09
11AB14	late	-20.03	9.03	10.56
11AB14	late	-18.24	10.35	11.02
13AB14	late	-20.38	10.20	10.78
13AB14	late	-19.66	11.82	13.08
15AB14	early	-20.56	8.51	10.31
15AB14	early	-20.40	9.03	10.83
15AB14	late	-19.64	10.99	11.71
15AB14	late	-20.17	10.73	12.03
15AB14	late	-19.80	10.97	12.27
21AB14	early	-20.20	8.98	10.64
21AB14	early	-19.93	11.34	13.00
21AB14	late	-19.49	12.25	12.97
25AB14	late	-18.85	9.79	10.69
25AB14	late	-18.60	10.76	11.66

[a]Values corrected to account for growth-induced depletion in $\delta^{15}N$ values.

Chapter 2. Accelerated energy intake increases survival rates of Black Oystercatcher broods[1]

2.1 Abstract

Black Oystercatchers (*Haematopus bachmani*), a species of conservation concern, depend on marine intertidal prey resources that are changing as a result of global climate change. To understand the relationship between Black Oystercatchers and the prey on which they depend, a study in southcentral Alaska was undertaken in 2013 and 2014 examining diet, feeding rates, brood growth and survival. To determine the importance of diet on brood survival, daily survival rates of broods were modeled as a function of energy intake rate (kJ min^{-1}) and other ecological factors. It was hypothesized that broods fed at accelerated energy intake rates would grow faster and fly earlier, thereby being less vulnerable to predators and have higher rates of survival. Consistent with our prediction, broods with higher energy intake rates had higher growth rates and daily survival rates. The best-supported model indicated that brood survival varied by energy intake rate, brood age, and total daily precipitation. To understand how adults meet the increasing nutritional needs of developing chicks, delivery rates, prey type and size were examined as a function of brood age. Delivery rates differed by age; however, the composition and the size classes of prey items fed to chicks by their parents did not, indicating that adults respond to the rising energetic needs of broods by increasing parental effort rather than switching prey. Collectively, these findings demonstrate the importance of diet and provisioning to broods, and given the consequences of reduced energy intake on survival, indicate that shifts in intertidal invertebrates as a result of climate change may have significant impacts on Black Oystercatcher populations.

[1]B. H. Robinson, L. M. Phillips, A. N. Powell. Accelerated energy intake increases survival rates of Black Oystercatcher broods. Prepared for submission to Waterbirds: The International Journal of Waterbird Biology.

2.2 Introduction

Black Oystercatchers (*Haematopus bachmani*) have been designated as a species of conservation concern due to small population size and unknown population trends, in addition to a limited distribution and high threats (U.S. Fish and Wildlife Service 2008). The global population is estimated at 10,000 individuals; however, accurate broad-scale population trends remain uncertain due to lack of systematic survey effort (Tessler et al. 2010; Andres et al. 2012). Black Oystercatchers range from Baja California, Mexico to the Aleutian Islands of Alaska and are reliant on nearshore marine habitats for all life history components including feeding, nesting, and raising young (Andres and Falxa 1995). This reliance on the nearshore environment throughout their annual life cycle has made them vulnerable to a number of threats including predation of eggs and young, coastal infrastructure development, human disturbance, direct and indirect effects of shoreline contamination (including reduction in food availability), and climate change with resultant effects on nesting and feeding resources (Tessler et al. 2010).

Despite considerable research effort examining threats to nest survival, our understanding of factors influencing Black Oystercatcher survival post-hatch is limited (Vermeer et al. 1992; Gill et al. 2004; Spiegel et al. 2012). For Black Oystercatchers, survival from hatching to fledging is the critical life-history stage (Groves 1984). Although predation is thought to be the major cause of mortality in Black Oystercatcher broods (Tessler et al. 2014), there is some evidence to suggest that diet plays an important role in brood survival. For example, in a study in British Columbia, heavier Black Oystercatcher chicks had a better chance of survival than lighter chicks (Groves 1984). Similar patterns were documented for Eurasian Oystercatchers (*H. ostralegus*), in that fledging success was positively correlated with growth rate (Kersten and

Brenninkmeijer 1995). Furthermore, in years of lower food availability, brood survival of Eurasian Oystercatchers decreased (Heg and van der Velde 2001).

Given the potential relationship between prey and brood survival, climate-induced changes in the abundance or composition of marine intertidal invertebrates may have substantial impacts on Black Oystercatchers. Warming sea-surface temperatures alter the behavior, physiology, and demography of many invertebrates on which Black Oystercatchers depend (Grenon and Walker 1981; Zwarts 1991; Dahlhoff and Menge 1996; Menge et al. 2008; Anestis et al. 2011). The breeding propensity of Black Oystercatchers has been found to be negatively correlated with sea-surface temperature, presumably due to warmer sea temperatures creating deficient feeding conditions, resulting in poor body condition of breeding adults (Hipfner and Elner 2013). Ocean acidification, sea level rise, and increased storm frequency may also impact marine invertebrate communities in the future (Harley et al. 2006; Fabry et al. 2008; Richardson 2008). These changes may have profound implications on Black Oystercatchers considering their diet is relatively specialized (Carney 2013) and has remained constant over the past century (B. Carney unpubl. data).

To assess the importance of diet on brood survival of Black Oystercatchers, we modeled daily survival rates of broods as a function of energy intake rate (kJ min^{-1}) and other ecological factors. We hypothesized that broods fed a similar diet but at a greater frequency would grow faster and fly earlier, thereby being less vulnerable to predators. If diet is an important factor influencing brood survival, we predicted energy intake rate of broods to be positively correlated with daily survival rates, and a parameter included in the top-ranking survival model. In addition to modeling daily survival rates, we determined fledging success and documented sources of chick mortality using remote-sensor cameras. To understand how adults meet the increasing

nutritional needs of developing chicks, we examined how delivery rates (number of prey items fed to chicks per minute), prey type, and size of prey that parents fed to broods varied by age. Collectively, these findings will identify the importance of diet and provisioning to the survival of Black Oystercatcher broods in a rapidly changing marine ecosystem.

2.3 Methods

2.3.1 Study area and field methods

Our field site was located within Kenai Fjords National Park in south-central Alaska, U.S.A., (59°51'18"N, 14°942'14"W). Specifically, we studied oystercatchers nesting in Aialik Bay, a deep, glacially-forged inlet, in-cut by smaller coves and bounded by steep mountains (Cook 1998; Spencer and Irvine 2004). Shoreline topography varies from gravel beaches of low-wave energy to rocky cliffs of high-wave energy with a mean tide range of 1.7 m (NOAA 2008).

Field Methods

From May to August in 2013 and 2014, we conducted systematic boat-based surveys of historically known nesting sites to locate breeding territories and oystercatcher broods. Upon detecting a territorial pair of Black Oystercatchers, we searched the surrounding area on foot. For all nests found, we recorded location, clutch size, and floated eggs to determine the stage of incubation (Mabee et al. 2006). We periodically revisited sites where nests had failed, sites where territorial pairs were observed but had yet to initiate a nest, and historical breeding sites to detect new nests throughout the breeding season. Once nests were located, we monitored them every three to five days throughout the nesting period. As nests approached the estimated day of hatch, we visited them daily to determine hatch date. After eggs hatched, we visited broods until they fledged or failed to determine growth rates, energy intake rates, and fledging success. We

monitored six broods in 2013 and 14 broods in 2014. Chicks were considered to have fledged when they were fully capable of sustained flight which occurred at ~ 40 days after hatch.

We marked chicks with colored tape or colored plastic bands until their tarsi were large enough to be fitted with a U.S. Geological Survey (USGS) metal band and two plastic alpha-numeric bands. We recaptured chicks every three to five days until chicks fledged or died in order to measure relaxed wing length to determine growth rates. We used wing growth rather than body mass in our growth rate analysis because wing length determines when chicks can fly (Tjørve et al. 2007).

In order to estimate energy intake rates, we conducted observations of adults provisioning their broods. We observed broods for two hours at low tide, when intertidal feeding grounds became exposed, approximately every three to five days until broods fledged or failed. Upon arriving at a territory, we located the brood from our boat using binoculars. During the first few days after hatch, most broods remained at the nest and later moved with their parents to intertidal feeding areas and throughout their territory. After a brood was located, we set up a 20-60x spotting scope in a camouflaged blind ~ 50 m away and waited for the birds to resume normal activity, which typically occurred within minutes of us entering the blind. We recorded the taxa and size class of each prey item fed to a chick and the time at which the provisioning event occurred. We assigned prey items to a size class in relation to adult bill length, using four size classes: 1 = <1/8, 2 = 1/8-1/4, 3 = 1/4-1/2, 4 = >1/2 the length of bill (Fig. 2.1). Prey items, in general, were easily identifiable to the genus or species level based on shape, size, and color of the prey, and handling behavior of the adults. If the observer was unsure of the prey or vision was obstructed during a feeding event, the prey item was listed as 'unknown'. Two observers worked together throughout the study to reduce observer bias.

In addition to direct observations, we also deployed infrared remote-cameras at nest sites to determine hatch date and identify other sources of mortality to broods. Previous research found that remote-cameras at oystercatcher nests do not alter the behavior of breeding pairs or attract animals to the territory (Spiegel et al. 2012). We used cameras placed approximately three meters from nests to monitor activity throughout incubation and the brood-rearing period. Although most broods left the nest site within a few days of hatch, we left the cameras at the nest site to detect the presence of potential predators in the general nesting area.

2.3.2 Energy analysis

We collected intertidal invertebrates to measure the energy content of Black Oystercatcher prey. We sampled from five intertidal feeding areas within our study site in July 2014. We collected the four most common prey items that we observed being fed to chicks: limpets (*Lottia* spp., n = 22), mussels (*Mytilus trossulus,* n = 30), barnacles (*Semibalanus cariosus,* n = 15), and chitons (*Katharina tunicata*, n = 10). Samples were frozen for approximately one month prior to being transported, in ice, to Fairbanks for laboratory analysis. Energy content was determined in the Barboza laboratory at the University of Alaska Fairbanks, Department of Biology and Wildlife. We measured prey length and mass, then dried samples in a freeze drier at -40°C for over 48 hours. After freeze-drying, we weighed the samples, removed shells, and reweighed the samples to determine dry mass. We combined samples of the same prey type to obtain three composite samples with minimum of 1 g of homogenized dry mass for each prey item; samples were then homogenized using scissors and a mortar and pestle. Energy content of composite samples was measured using a bomb calorimeter and corrected for the unburned fuse and acid by titration. We calculated the energy density of composite samples as

kilojoules per gram dry mass (kJ g^{-1} DM) and averaged composite samples of the same prey type to obtain mean energy densities.

Since not all organic compounds in the diet are available to the consumer, we conducted a pepsin digestibility assay to determine the digestible energy density of prey items (Barboza et al. 2008). Approximately 1 g of homogenized dry mass of each prey type was placed in synthetic filter bags, inserted in jars, and immersed in an acid-pepsin solution of pH 1 in a 0.1 mol/L HCl solution containing 2 g/L pepsin (1:10000 (10000 IU/mg); VanSomeren et al. 2015). The jars were placed in an incubator for six hours, then filter bags were removed, rinsed, and dried in an oven. We reweighed the samples to determine the remaining mass. Digestibility of prey was calculated as the difference in total dry mass and remaining dry mass divided by total dry mass. We calculated digestible energy density of prey items as the product of energy density and digestibility.

We estimated energy intake rates of broods based on our provisioning observation data and digestible energy density estimates. For each prey type, we estimated the energy content of the four sizes classes to which observed prey was assigned. Energy content (kJ) of size classes was calculated as the product of digestible energy density (kJ g^{-1}) for each prey type and dry mass (g). We estimated the dry mass of size classes using the length to mass regression of each prey type and the proportion of bill length that each size class represented. We used adult bill length data from Jehl (1985; in Andres and Falxa 1995) and calculated length to mass regressions from our measurements following Burgherr and Meyer (1997; in Baumgärtner and Rothhaupt 2003). Energy intake rate for each observation was calculated as the total energy content of prey fed to chicks per time observed (kJ min^{-1}). Delivery rate for each observation was calculated as the total number of prey items fed to chicks per time observed. To account for

variation in brood size, which ranged from one to three chicks, we divided energy intake and delivery rates by the number of chicks in a brood. We averaged energy intake rates of observations to obtain a mean energy intake rate for each brood.

We calculated linear growth rate to quantify wing growth (Nisbet et al. 1995). Although birds exhibit a nonlinear pattern of growth (Ricklefs 1973) we were unable to capture chicks after they fledged, when growth rates begin to asymptote. Therefore, we analyzed the linear phase of growth which occurs when Black Oystercatchers are 5 to 35 days old (Groves 1984; Hazlitt et al. 2002). Growth rate coefficients were calculated for broods by linear regression of age (in days) and wing length (mm). Age and wing length values were log-transformed to meet assumptions of normality and equal variance. To test for a relationship between energy intake and wing growth, we conducted a linear regression of energy intake rate and wing growth rate coefficients.

We examined the relationship between delivery rate (prey items fed to chicks per minute) and chick age (in days) first by plotting delivery rates as a function of age. Delivery rates were log-transformed to meet normality. The data showed an asymptotic relationship with delivery rate increasing for the first ~15 days then leveling off afterwards. Because of this relationship, we split the data into two groups, early (before the asymptote, at 15 days old and younger) and late brood-rearing period (older than 15 days), and tested for a difference in delivery rates between the groups using a two-sample t-test. We conducted a Chi-squared test of independence to determine if prey items (limpets, mussel, barnacle, chiton, 'other' prey, unknown prey) consumed by chicks differed between the early ($\leq$15 days) and late brood-rearing period (>15 days). We also conducted a Chi-squared test to determine if the four size classes of prey consumed by chicks differed between brood-rearing periods.

2.3.3 Survival analysis

We used an information-theoretic approach to examine relative support of models describing associations between daily survival rate of broods and variables of interest. A small set of candidate models was selected using a multi-step approach (Lebreton et al. 1992). We began by modeling daily survival rates of broods relative to year and age; we modeled brood age as both a linear and quadratic trend. We did not consider linear or quadratic temporal trends because they may be confounded with age (Dinsmore et al. 2002). After selecting the best-supported model in this set, we included abiotic factors we considered might influence survival. These included weather covariates (total daily precipitation and minimum daily temperature) and a categorical covariate describing landform (island vs. mainland). We reasoned that survival would be higher for broods on islands than the mainland due to the absence of mammalian predators on islands in our study area. After selecting the best-supported model from this set, we added two additional individual covariates: brood size and our primary variable of interest, energy intake rate. Given that energy intake rates increase with brood age (Hazlitt et al. 2002) and we did not have intake rates for many broods 20-40 days old because they did not survive to fledge, we limited our energy intake rates of broods to observations that occurred when broods were 15 days old or younger. In addition, we were unable to obtain energy intake rates for seven of the 20 broods studied. To account for these missing data in our model that included energy intake rate, we only applied the energy intake rate covariate to the 13 broods with energy intake data and applied the other covariates in the model to all 20 broods (Cooch and White 2002). We used Akaike's information criterion adjusted for small sample size (AIC_c) and normalized Akaike weights (w_i) to select the top support model in the candidate set. We conducted our survival analysis using the nest survival module in program MARK, version 6.2; all other

statistical analyses were done in program R, version 3.1.1 (White and Burnham 1999; R Development Core Team 2014).

2.4 Results

We monitored a total of 20 Black Oystercatcher broods in 2013 and 2014. Mean brood size was 2.3 chicks (± 0.7 SD) with a range of 1-3 chicks per brood. Of 20 nests that hatched, 10 fledged at least one chick (fledging success of 50%). Because most broods left the nest area within three days of hatch, remote-sensor cameras only documented one brood depredation event; a Peregrine Falcon (*Falco peregrinus*) preying upon newly hatched chicks. Remote-sensor cameras also detected the presence of a black bear (*Ursus americanus*), domestic dogs (*Canis familiarus*), and Glaucous-winged Gulls (*Larus glaucescens*) near nest sites of failed broods.

We observed 1979 prey items fed to chicks in the 20 broods. Limpets were the most common prey consumed followed by mussels, barnacles and chitons. Of the common prey consumed by Black Oystercatcher broods, limpets had the highest energy density (mean ± SD; 19.99 ± 0.40 kJ g^{-1} DM) of the four prey items we analyzed (Table 2.1). However, mussels had the highest digestibility (0.89 ± 0.04 g digested g^{-1} DM) and digestible energy density (16.02 kJ g^{-1} DM). Prey items of size class 2 (1/8-1/4 bill length) made up the majority (53%) of prey items fed to chicks. Digestible energy content of this size class was highest for limpets (1.13 kJ), followed by chitons (0.66 kJ), barnacles (0.59 kJ) and mussels (0.35 kJ).

Delivery rates were higher during the late brood-rearing period than the early brood-rearing period (t_{17}= -3.39, P = 0.004; Fig. 2.2). Neither the composition (X^2_{25} = 30, P = 0.22) nor the size classes (X^2_9 = 12, P = 0.21) of prey items fed to chicks by their parents differed between early and late brood-rearing periods.

We calculated wing growth rates for 12 broods during the linear phase of growth. The mean wing growth rate coefficient was 1.12 (± 0.12 SD) with a range of 0.87 – 1.27. Energy intake rate to day 15 varied among broods, ranging from 0.01 – 1.01 kJ min^{-1} with a mean of 0.28 (± 0.26 SD; n = 13). Energy intake rates were positively correlated with wing growth rate coefficients ($F_{1,9} = 14.87$, $P = 0.004$; Fig. 2.3).

We modeled daily survival rates of 20 Black Oystercatcher broods. The best-supported model indicated that brood survival varied by energy intake rate, brood age, and total daily precipitation (Table 2.2). Support for a model with energy intake rate was strong; normalized Akaike weight indicated a 0.91 probability that it was the best model of the candidate models. This model was 7.41 AIC_c units better than the next best model, which did not include energy intake rate. Energy intake rates were positively correlated with daily survival rates (Fig. 2.4). The age covariate in the top-ranking model was quadratic, with daily survival rates increasing for the first two weeks of hatch and decreasing after three weeks (Fig. 2.5).

2.5 Discussion

Our results supported our hypothesis that broods fed at accelerated energy intake rates would grow faster, and have higher rates of survival. Consistent with our prediction, broods with higher energy intake rates had higher daily survival rates. Furthermore, the addition of an energy intake rate parameter to the top model improved model fit and strongly decreased model deviance. Broods provisioned at higher energetic rates had higher rates of wing growth, presumably enabling them to fly at an earlier age, possibly making them more adept at evading predators. In another study that examined chick survival of Black Oystercatchers pre- and post-fledging, all mortalities occurred before chicks began to fly (Groves 1984). Birds that can

minimize the period in which they are most vulnerable to predators can increase their chances of survival. However, under conditions of restricted energy intake, growth is compromised, leading to negative effects on survival. Our results underscore the importance of diet and provisioning to the growth and survival of Black Oystercatcher broods.

The relationship that we found between energy intake rate and growth and survival is consistent with findings from other waterbird studies. Arctic shorebird chicks that had access to higher prey abundances had higher growth rates than chicks with lower prey availability (McKinnon et al. 2012). African Black Oystercatchers (*Haematopus moquini*) with low biomass available in their territories had decreased energy intake rates and were less likely to successfully raise two chicks (Leseberg et al. 2000). Food supply also strongly affected the growth and productivity of marine birds including kittiwakes (*Rissa* sp.) and skuas (*Stercorarius* sp.) (Gill and Hatch 2002; Ritz et al. 2005).

Although energy intake rates were positively correlated with wing growth, other mechanisms associated with feeding rates, aside from growth, may simultaneously be influencing survival. Chicks with higher energy intake rates may also have better body condition making them more resistant to severe weather and disease (Moller et al. 1998); however, we did not encounter any diseased chicks. Additionally, parents that feed chicks at higher rates may attend to chicks more frequently and be able to defend them from predators more often. Since we were not able to test these hypotheses, we cannot rule out the possibility that additional mechanisms associated with intake rate, aside from growth, impact brood survival.

In addition to energy intake rate, parameters in the best-supported survival model included brood age and daily precipitation. The age trend in this model was quadratic with survival rates low at hatch, increasing for the first two weeks, then leveling off and decreasing

after three weeks. The pattern of lower survival among younger chicks has also been found in other shorebirds including American Oystercatchers, Snowy Plovers (*Charadrius nivosus*) and Western Sandpipers (*Calidris mauri*; Ruthrauff and McCaffery 2005; Colwell et al. 2007; Schulte 2012). Young chicks are slow and small, making them more vulnerable to predators and severe weather. Yet, in our study, after survival rates increased, they leveled off and decreased after three weeks. Chicks become less vulnerable to weather as they develop and begin to thermoregulate; however they also become more active and conspicuous to predators. Although chicks can move relatively quickly, it is unlikely that they can outrun predators. These combined factors may explain the quadratic relationship between age and survival.

Fledging success in our study was low but comparable to estimates reported for Black Oystercatchers in other studies (Vermeer et al. 1992; Andres and Falxa 1995; Hazlitt 2001; Morse et al. 2006). Although evidence of specific predators is difficult to obtain, we documented a Peregrine Falcon preying on young chicks. To our knowledge this is the first study to document a depredation event on chicks. Remote-sensor cameras also documented domestic dogs depredating a Black Oystercatcher nest and running loose on beaches where chicks were present (Robinson and Phillips 2013), highlighting one way in which human-related disturbance impacts Black Oystercatcher productivity.

Our findings also highlight how adults respond to the increasing nutritional needs of developing chicks. Adults did not adjust the types of prey or size classes brought to chicks during the early and late brood-rearing periods, instead they increased the frequency by which they delivered prey to chicks. Experimental studies of chick provisioning in other species revealed a similar trend; individuals adjusted their feeding rate to account for temporary changes in the energetic demands of broods but did not adjust the bolus size of food items brought to the

nest (Koenig and Walters 2012). Together, these results show that adults respond to the rising energetic needs of broods by increasing parental effort.

Our study demonstrates the importance of diet and provisioning to the survival of Black Oystercatcher broods. Given the consequences of reduced energy intake on brood survival, shifts in composition and abundance of intertidal invertebrates as a result of climate change may have significant impacts on Black Oystercatcher populations. Brood survival, productivity and recruitment into the breeding population may experience declines in the future if marine intertidal invertebrates respond negatively to warming sea temperatures, ocean acidification, sea level rise, and increased storm frequency. To better understand the biology underlying Black Oystercatcher conservation, future research should address how climate-driven changes in nearshore ecosystems will affect food resources and predator communities with respect to oystercatcher populations.

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Committee approval (# 436591). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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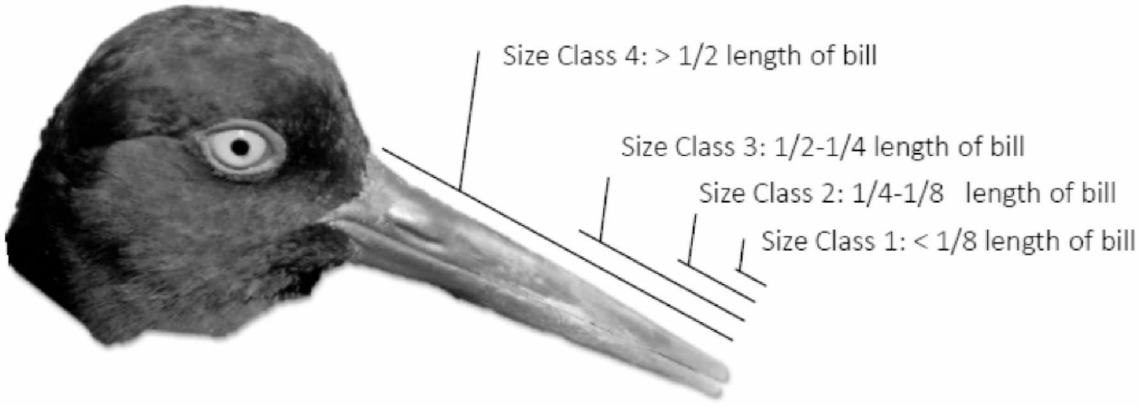

Figure 2.1. Classification scheme used to assign prey items to size classes using the bill length of Black Oystercatchers.

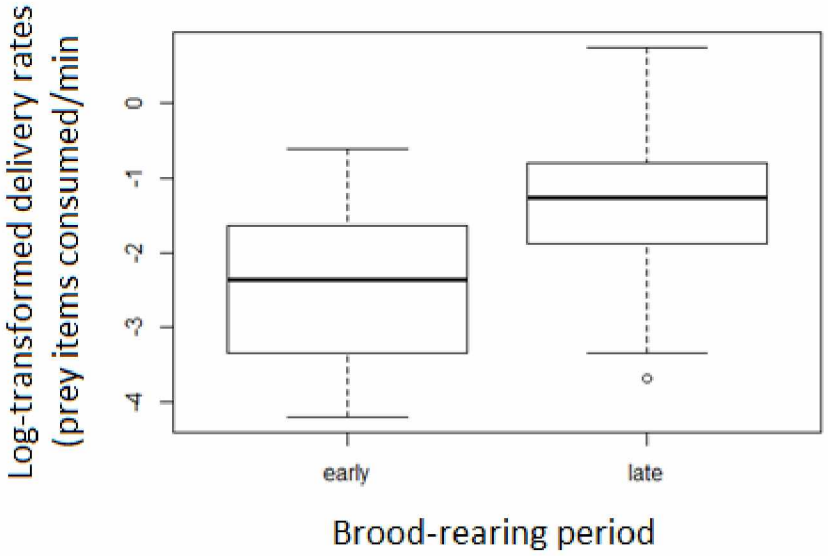

Figure 2.2. Log-transformed delivery rates (prey items consumed per minute) of Black Oystercatcher broods differ between early (less than 15 days old) and late (15 days or older) brood-rearing period in Kenai Fjords National Park, Alaska. Boxes represent the distances between the first and third quartiles; center bars represent the medians.

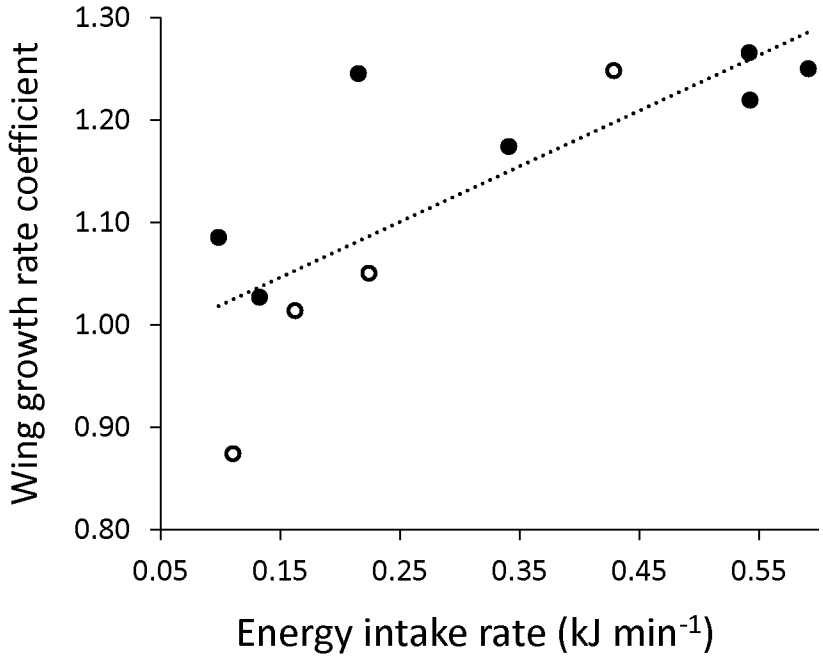

Figure 2.3. Wing growth rate coefficients as a function of energy intake rate for Black Oystercatcher broods that survived to fledge (closed circles) and died before fledging (open circles) in Kenai Fjords National Park, Alaska, 2013-2014: slope = 0.55 (± 0.14 SD), $r^2 = 0.58$, n = 11).

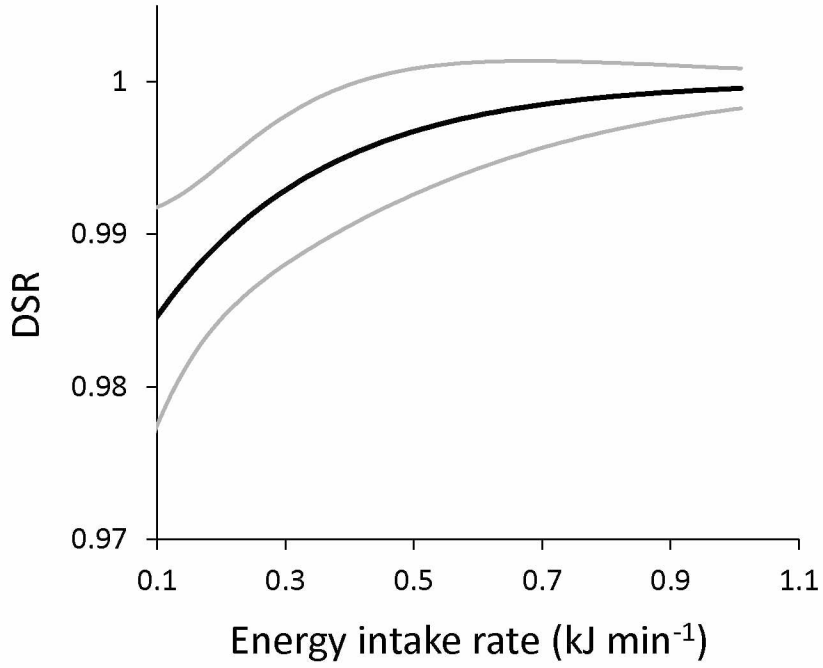

Figure 2.4. Predicted daily survival rates (DSR) as a function of energy intake rate of Black Oystercatcher broods in Kenai Fjords National Park, Alaska, 2013-2014. Grey lines represent ± SD.

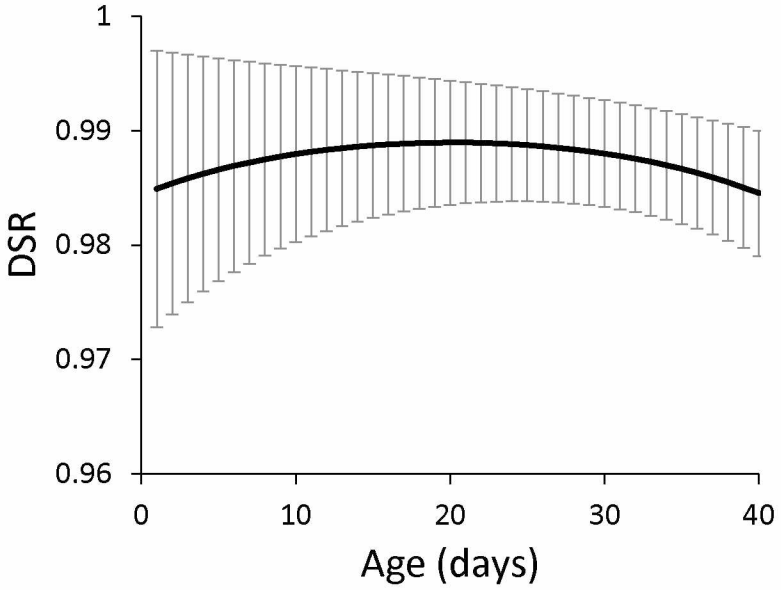

Figure 2.5. Daily survival rates (DSR) of Black Oystercatcher broods by age in Kenai Fjords National Park, Alaska, 2013-2014. Intervals represent ± SD.

Table 2.1. Energy density (kJ g^{-1}) and digestibility (g digested g^{-1} dry mass) of intertidal marine invertebrates collected in Kenai Fjords National Park, Alaska, July, 2014.

	Energy density of composite samples						Mean energy density (kJ g^{-1}) ± SD	Mean digestibility (g digested g-^{1} DM) ± SD	Mean digestible energy density (kJ g^{-1} DM)
	kJ g^{-1}	*n*	kJ g^{-1}	*n*	kJ g^{-1}	*n*			
Barnacle	18.64	5	16.96	5	17.58	5	17.73 ± 0.69	0.49 ± 0.02	8.64
Chiton	18.68	3	18.38	3	19.65	4	18.90 ± 0.54	0.73 ± 0.11	13.75
Limpet	19.59	10	20.39	12	-	-	19.99 ± 0.40	0.78 ± 0.08	15.57
Mussel	17.84	15	18.06	15	17.94	15	17.95 ± 0.09	0.89 ± 0.04	16.02

Table 2.2. Model rankings for Black Oystercatcher brood survival at Kenai Fjords National Park, Alaska, 2013-2014. Models were ranked by differences in Akaike's Information Criterion for small sample size (ΔAIC_c) values. Normalized Akaike weight (w_i), number of parameters (K), and model deviance (Deviance) are also shown for each model.

Model	ΔAIC_c[a]	w_i	K	Deviance
Age^2 + Daily Precip + Energy Intake Rate	0.00	0.91	9	59.12
Age^2 + Daily Precip	7.41	0.02	4	76.77
Age^2	7.97	0.02	3	79.35
Age^2 + Daily Precip + Min Daily Temp	8.29	0.01	5	75.61
Age^2 + Daily Precip + Brood Size	9.19	0.01	5	76.51
Age^2 + Min Daily Temp	9.77	0.01	4	79.13
Age^2 + Landform	9.98	0.01	4	79.34
Year	10.99	0.00	2	84.40
Year + Hatch Date	11.00	0.00	3	82.39
Constant	11.17	0.00	1	86.59
Age	12.33	0.00	2	85.73

[a]The lowest AICc score in the model set was 77.43

General Conclusions

My thesis addressed the feeding ecology of Black Oystercatcher (*Haematopus bachmani*) chicks by characterizing chick diet and examining age- and habitat-specific variation in diet. Additionally, I assessed methods used to characterize chick diet and examined the importance of prey and provisioning to chick survival. I addressed these research objectives by studying the diet of a population of Black Oystercatchers in Kenai Fjords National Park, Alaska during the breeding seasons in 2013 and 2014.

I characterized the diet of Black Oystercatcher chicks using three methods: quantification of prey remains at nest sites, direct observation of adults feeding young, and diet reconstruction by stable isotope analysis. Similar to other studies of Black Oystercatchers in Alaska and Canada, I found that chicks were fed a diet based primarily of limpets (*Lottia* spp., *Acmaea mitra*) and mussels (*Mytilus trossulus*), supplemented with other intertidal invertebrates (Hartwick 1976; Andres and Falxa 1995; Andres 1998; Hazlitt et al. 2002). I found no relationship between diet and age of chicks. However, I did find that chick diet differed between habitat types; specifically, mussels were more common in the diet of chicks on rocky islands whereas limpets were more common in the diet of chicks on gravel beaches. To my knowledge, this is the first study to investigate habitat-specific differences in Black Oystercatcher chick diet. However, research on Eurasian Oystercatchers (*H. ostralegus*) found diet differences between pairs that nest near the coast versus inland (Safriel 1985). Together, these findings indicate that diet specializations exist within oystercatcher populations.

To better understand the biases and limitations associated with the quantification of prey remains, I compared diet estimates from the quantification of prey remains with two other

methods commonly used to characterize diet: direct observation of adults feeding young and diet reconstruction by stable isotope analysis. When compared with other methods, estimates from collected prey remains over-represented the proportion of limpets in the diet, slightly under-represented the proportion of barnacles, and failed to detect soft-bodied prey such as worms. These findings can help inform researchers when selecting a method to study or monitor diet. For example, if they need to detect all prey including soft-bodied organisms they should avoid using the quantification of prey remains. However, if they are looking for an inexpensive method to provide a quick estimate of diet, then the use of prey remains may be considered. Prey remains have also recently been used to document the Northern abalone (*Haliotis kamtschatkana*) as oystercatcher prey, which previously has never been reported (Bergman et al. 2013). This example illustrates that prey remains, although biased in some regards, can still provide valuable data.

For my second chapter, I examined diet and provisioning with respect to chick growth and survival. Of all the prey items I measured, limpets and mussels had the highest digestible energy density. This finding provides a plausible explanation for why limpets and mussels had the highest proportions in our chick diet estimates and further illustrates the importance of these prey items to oystercatchers. Because limpets and mussels have higher digestible energy density than other prey, parents can meet the energetic needs of chicks more quickly by feeding limpets and mussels to chicks as opposed to other prey of the same size. The value of limpets and mussels to Black Oystercatcher chicks is increasingly evident when considered in the context of energy intake rates. I found that chicks with higher energy intake rates had higher daily survival rates than chicks with lower intake rates. Time-energy models for African Black Oystercatchers (*H. maquini*) have shown that when intake rates are low, oystercatchers regularly encounter

difficulties rearing multiple chicks (Leseberg et al. 2000). Furthermore, food supply strongly affects the growth and productivity of other seabirds as well (Gill and Hatch 2002; Ritz et al. 2005). Although diet plays an important role in chick survival, ongoing changes in nearshore marine ecosystems may threaten both intertidal invertebrate and Black Oystercatcher populations.

Global climate change is altering sea temperature, ocean chemistry, sea level, and ocean currents (Harley et al. 2006). These changes have already begun to impact intertidal invertebrates. Increasing sea surface temperature is believed to be responsible for the contraction in the southern limit of the range distribution of a northerly limpet species, *Lottia digitalis*, and the northward expansion of *L. austrodigitalis*, a southerly limpet species (Crummett and Eernisse 2007). Long-term monitoring of marine intertidal invertebrates has detected an apparent decrease in percent cover of mussels in Kenai Fjords and Katmai National Parks, and Prince Williams Sound, which may be related to climate change (H. Coletti, unpublished data). Considering the relationship between energy intake rate and chick survival, these changes may impact Black Oystercatcher populations on a large scale.

In light of these changes, it is imperative that managers proactively work towards the conservation of Black Oystercatchers. One way in helping to achieve this is through continued monitoring of Black Oystercatcher diet. By detecting when the relative abundance of prey is low, long-term monitoring of diet can be useful in identifying when chick survival is compromised. Diet monitoring can also inform managers how oystercatchers are responding to shifts in invertebrate abundance. Stable isotope analysis proved useful in detecting diet shifts in adult and chick African Black Oystercatchers as a result of the invasive Mediterranean mussel (*Mytilus galloprovincialis;* Kohler et al. 2009). My thesis work is the first to show that stable isotope

analysis can successfully be used to characterize the diet of Black Oystercatcher chicks and indeed this technique could be useful in detecting diet shifts within the species. Considering the ease and low cost of using prey remains to infer diet, the quantification of prey remains can be another useful tool to monitor the Black Oystercatcher diet given that biases are accounted for before making interpretation of trends in the diet data. Combining diet estimates from the quantification of prey remains and another method such as direct observation or stable isotope analysis is potential solution for managers seeking higher quality data for less cost and effort.

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